

# NEW ANTIARCHS (DEVONIAN PLACODERM FISHES) FROM QUEENSLAND, WITH COMMENTS ON PLACODERM PHYLOGENY AND BIOGEOGRAPHY

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Two new antiarchs are described from the Middle Devonian of the Broken River area of northern Queensland. *Wurungulepis denisoni* gen. et sp. nov. is an asterolepidoid represented by a single articulated trunk armour with associated pectoral fin bones and scales. It is referred to the family Pterichthyodidae, and most closely resembles the European genus *Gerdalepis*, but its trunk-armour proportions and scales are distinctive. The specimen is important in demonstrating the association of micro- and macrovertebrate remains in a single taxon of probable Eifelian age. *Nawagiaspis wadeae* gen. et sp. nov. came from a higher horizon in the Broken River Formation, of probable Givetian age. It combines various morphological characters previously regarded as typical of the asterolepidoids (e.g. tubercular ornament, no preorbital recess, short endocranial postorbital processes), or of the bothriolepidoids (prelateral plate, articular process on submarginal plate, anterior dorsolateral and posterior ventrolateral plates with common suture). It is referred to the latter group on the evidence of the cheek attachment. New information is provided on the structure of the jaws and cheek in antiarchs.

□ Devonian, placodermis, antiarchs, Pterichthyodidae, Bothriolepidoidei, phylogeny, biogeography, Queensland, *Wurungulepis*, *Nawagiaspis*, Broken River Formation.

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The antiarchs are a group of placoderm fishes well represented in Late Devonian strata throughout the world. They have been known from Australia since Hills (1929) described the species *Bothriolepis gippstandiensis* from the Upper Devonian rocks of eastern Victoria. From Queensland it was again Hills (1936) who first reported an antiarch from the Middle - Late Devonian near Gilberton, and recently other isolated occurrences have been listed by Turner (1982). Probably the oldest antiarch occurrence yet known from Australia is an asterolepid antiarch from the Cravens Peak Beds (Early-Middle Devonian) of the Georgina Basin in western Queensland (Young, 1984a).

In this paper two new antiarchs are described from the Broken River area of northern Queensland (Fig. 1). They are of interest in being of Middle rather than Late Devonian age, in their occurrence in marine limestones rather than fluvial or lacustrine deposits in which antiarchs are most common, and in their excellent preservation. Although somewhat distorted, they are uncrushed, and their preservation in limestone has permitted preparation using the acetic acid technique to completely remove skeletal remains

from the matrix. *Nawagiaspis wadeae* gen. et sp. nov., described below, provides morphological details on structures otherwise only known in a very few antiarchs. This specimen was collected by Dr Mary Wade from the Broken River Formation. The geology of this region has been summarised by Wyatt and Jell (1980), and the biostratigraphy of the Devonian sequence discussed by Mawson *et al.* (1985), and Mawson (1987). The second specimen came from the same region, but in slightly older Middle Devonian rocks.

Both specimens are housed in the Queensland Museum (prefix QMF). The prefix L signifies a University of Queensland locality number. Standard abbreviations for bones of the antiarch dermal skeleton as used in the text and figures are listed below.

## ABBREVIATIONS

ADL	anterior dorsolateral plate
AMD	anterior median dorsal plate
AVL	anterior ventrolateral plate
ad1,2	anterior and posterior articular processes on SM

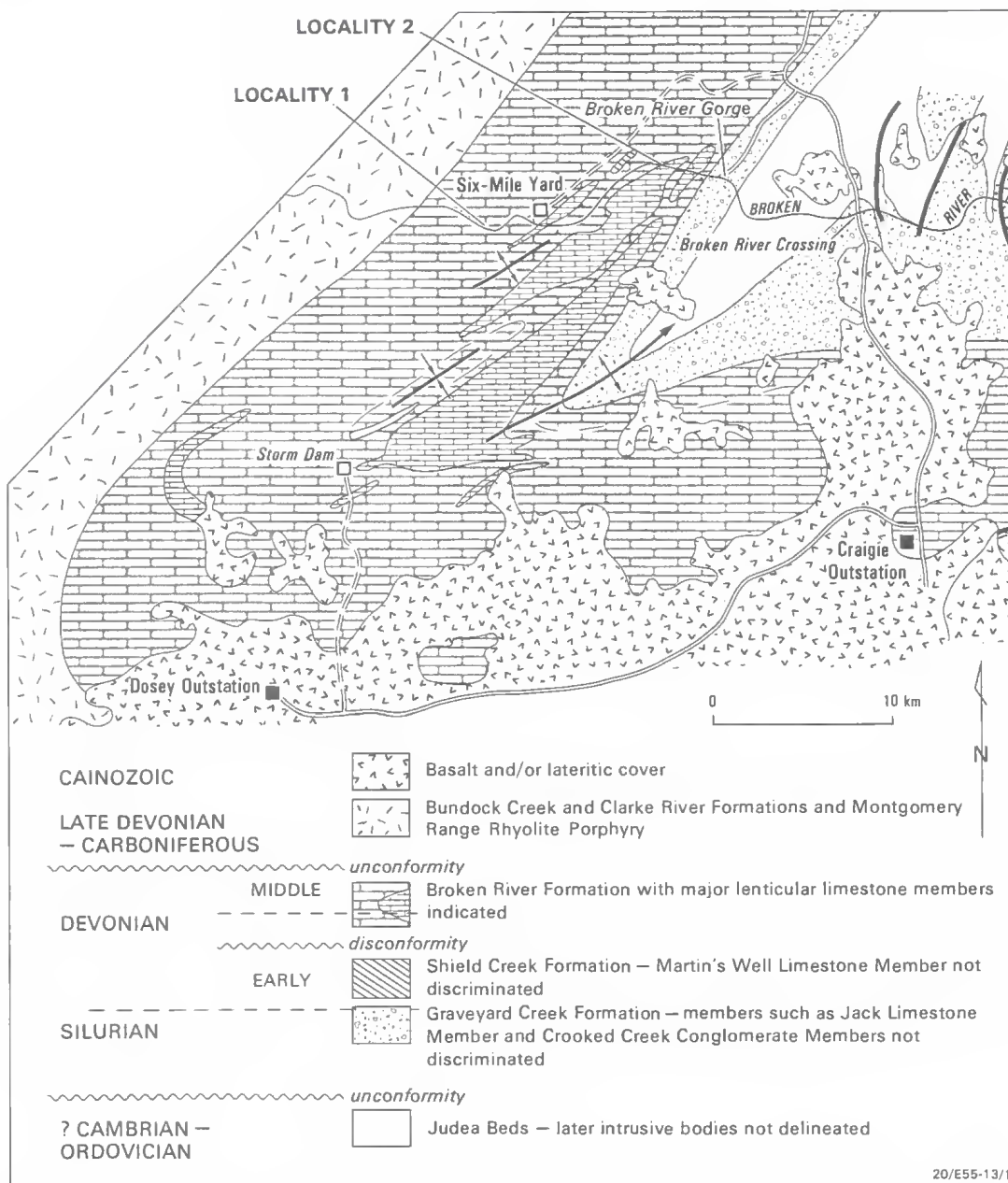


FIG. 1. Geology of the Broken River area, showing type localities for new taxa described in this paper (modified after Mawson *et al.*, 1985).

art	articular facet adjacent to axillary foramen	dma	tergal angle of trunk-armour
av	ventral articular area of SM plate	dmr	dorsal median ridge of trunk-armour
cit	crista transversalis interna anterior	f.ap	fossa articularis pectoralis
cr	median ventral crest on AMD	f.ax	foramen axillare of AVL
cr.tp	crista transversalis interna posterior	fe.orb	orbital fenestra
dlr	dorsolateral ridge of trunk-armour	gr. ul	groove for upper lip
		ifcl	principal section of infraorbital sensory

	line on head-shield
ifc2	branch of infraorbital sensory line diverging on L
ifc3	section of infraorbital sensory line on suborbital plate
L	lateral plate
lcg	main lateral line groove
ln	lateral notch of head-shield
lpr	lateral process of head-shield
MxL	mixilateral plate
mvr	ventral median ridge of dorsal wall of trunk-armour
Nu	nuchal plate
nn	nasal notch on first sclerotic plate
oa.ADL	area overlapped by ADL
oa.MxL	area overlapped by MxL
ood	otico-occipital depression of head-shield
orb	orbital notch of L plate
PDL	posterior dorsolateral plate
PL	posterior lateral plate
PM	postmarginal plate
PMD	posterior median dorsal plate
PNu	paranuchal plate
PrL	prelateral plate
PrM	premedian plate
PVL	posterior ventrolateral plate
proc	preobstantic corner of head-shield
pr.po	depression on head-shield for dorsal face of endocranial postorbital process
prv2	posterior ventral process of dorsal wall of trunk-armour
psoc	postsuborbital sensory groove
pt1	anterior ventral pit of dorsal wall of trunk-armour
pt2	posterior ventral pit of dorsal wall of trunk-armour
SM	submarginal plate
SR	skull-roof
sal	subanal lamina of PVL plate
scl.I-3	sclerotic plates I-3
soc	supraorbital sensory groove
vlr	ventrolateral ridge of trunk-armour

## SYSTEMATIC DESCRIPTIONS

Class PLACODERMI

Order ANTIARCHI

Suborder BOTHRIOLEPIDOIDEI Miles (1968)

*Nawagiaspis* gen. nov.

### ETYMOLOGY

After the Nawagi aboriginal tribe, one of the original tribes of the Broken River area.

### DIAGNOSIS

A bothriolepid of moderate size, with tuberculate ornament on dermal bones sometimes arranged in radiating ridges. Skull probably with a short obstantic margin, preorbital recess absent or very shallow, and otico-occipital depression deep with endocranial postorbital processes terminating posterolateral to orbital fenestra. Suborbital plate short and high, with two notches and a small posteroventral process on its lateral margin. Biting margins of both jawbones lacking denticulation. Submarginal plate elongate, with a strong anterodorsal articular process. Prelateral plate triangular, with a pronounced anterior process and dorsal and posterior margins oriented normal to each other. Trunk armour short and high; posterior median dorsal with very strong ventral process and median ventral ridge. Anterior dorsolateral in sutural contact with posterior ventrolateral plate. Posterior dorsolateral and posterior lateral incompletely fused. Postbranchial lamina of anterior ventrolateral strongly developed, and axillary foramen small.

### REMARKS

*Nawagiaspis* is distinguished from most other bothriolepidoids by its short endocranial postorbital processes, from *Bothriolepis* by its tuberculate ornament, from *Grossilepis* by the shape of the anterior median dorsal plate and various other features, from *Monarolepis* (= *B. verrucosa*; see Young, 1988) and probably *Dianolepis* by the strong posterior ventral process and ridge beneath the posterior median dorsal plate, and from *Microbrachius* and *Wudinolepis* by the absence of a preorbital depression. The species *Bothriolepis warreni* differs from other *Bothriolepis* species and resembles *Nawagiaspis* in its tuberculate ornament and short postorbital processes (Long & Werdelin, 1986, fig. 29), but other differences (e.g. skull shape, strong posterior ventral process) indicate that they are not closely related. The characters by which *Nawagiaspis* is placed in the suborder Bothriolepidoidei, and distinguished from non-bothriolepidoid antiarchs, are dealt with below.

*Nawagiaspis wadeae* sp. nov.

(Figs 2-7, 8A, 9-11)

### ETYMOLOGY

After Dr Mary Wade, Queensland Museum, who collected the specimen.

## HOLOTYPE

QMF16592, an articulated incomplete skull and trunk-armour with associated dermal bones of the cheek, jaws and sclerotic ring.

## LOCALITY

L4428, a small limestone outcrop on eastern side of gully 1 km upstream from Six Mile Yard, grid reference 596442, Burges 1:1,000,00 map (locality 1, Fig. 1).

## HORIZON

Broken River Formation, Middle Devonian, probably Givetian (J.S. Jell, pers. comm.).

## DIAGNOSIS

As for genus (only species).

## REMARKS

Some of the features included in the diagnosis above are no doubt specific features, which can be further analysed should additional specimens be discovered.

## DESCRIPTION

As collected, the dorsal, right lateral, and ventral surfaces had been exposed to weathering on the surface of a limestone nodule, and portions of the dermal bone were lost. Gaps were filled with plastic which in some cases preserved the visceral bone surface intact after acetic acid preparation. The cheek, jaw, and sclerotic bones fell away from the

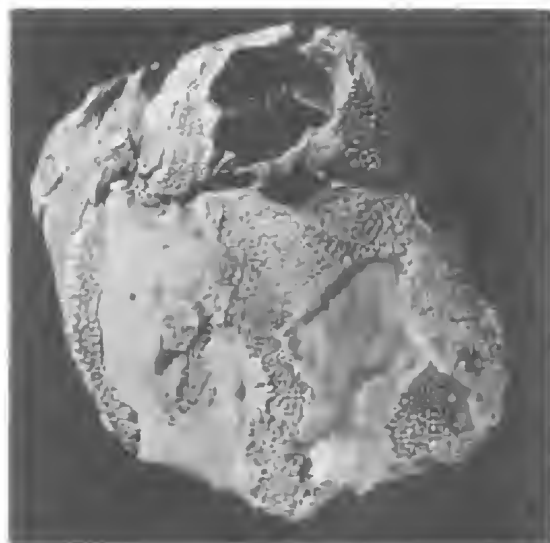


FIG. 2. *Nawagiaspis wadeae* gen. et sp. nov. Holotype, QMF16592, incomplete skull roof and trunk-armour in dorsal view ( $\times 0.85$ ).

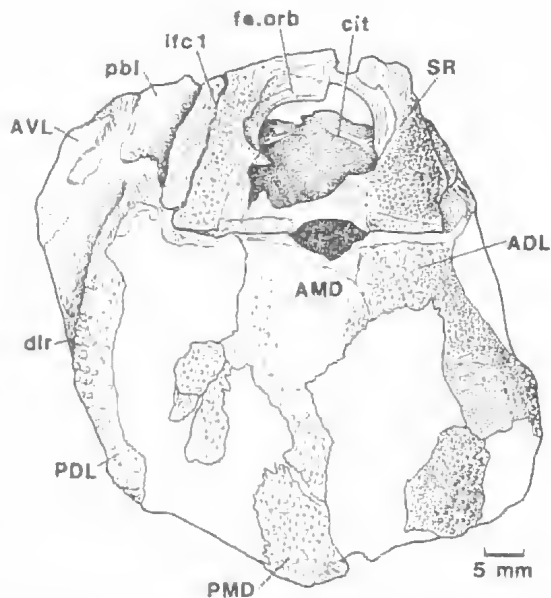


FIG. 3. *Nawagiaspis wadeae* gen. et sp. nov. Holotype in dorsal view (QMF16592).

skull during preparation, but the rest of the specimen remained intact (Fig. 2).

The skull has incomplete margins except for the region of the neck-joint articulation. It is preserved with only slight displacement in its articulated position against the trunk-armour, so an outline restoration can be derived from surrounding structures. The left SM plate has a very close fit on the postbranchial part of the AVL (Fig. 10), and gives a reliable indication of the preorbital length of the skull, this being very incompletely preserved (Fig. 4A). In antiarchs generally a branch of the infraorbital sensory canal passes laterally off the skull-roof onto the prelateral plate of the cheek. The latter is preserved with its sensory groove (see below), and restored in its position in front of the SM plate (PrL, Fig. 4A) gives the approximate position of this branch on the skull roof. The main sensory groove on the skull is directed anteromesially from the neck-joint articulation (ifc1, Fig. 4), but at its anterior preserved end shows a lateral flexure which may be extended to the branching point of the lateral branch of this canal (ifc2). It is also evident from the configuration of the dorsal (mesial) ornamented edge on the SM plate (see below) that the skull had a lateral process (lpr) behind which was a lateral notch (ln) equivalent to the 'supraspiracular' notch of Stensiö (1948). However, the shape of the prelateral plate (see below) indicates that the prelateral notch of the

skull was probably absent. The obstantic margin is obscured on the left side of the specimen by the AVL plate, and is broken away on the right (Fig. 3), but the general shape of the skull as restored suggests that it was relatively short. The close fit of the SM against the AVL, as noted above, suggests that there was no posterolateral extension of the PM plates of the skull. Finally, the smooth area along the anterior margins of the ADL and AMD plates of the trunk suggest a broad obtected nuchal area and convex posterior margin to the skull (Fig. 4B).

The visceral surface of the skull shows no sign of a preorbital recess. There is a strong paramarginal crista on both sides which fuses with the convexity surrounding the orbital fenestra such that the recess for the anterior postorbital process is a short notch posterolateral to the orbit (pr.po, Fig. 4B). A low

thickening on the bone extends anterolaterally from the postorbital process past the orbital fenestra (as far as preserved). The otico-occipital depression (ood) is delimited posteriorly by a strong transverse nuchal crista which, as far as preserved, has similar configuration to that of *Asterolepis ornata* (Stensiö, 1931, fig. 15). However, there is no sign of an extra ridge running laterally from the paramarginal crista, as occurs on the lateral plate of *Asterolepis* (e.g. Stensiö, 1931, fig. 8). This was interpreted by Young (1984b) as a remnant of the posterior postorbital process. The approximate limits of the endocranial impressions on the visceral skull surface are indicated in Fig. 4B.

Four sclerotic bones were retrieved from inside the skull cavity during preparation. Because of their small size and delicate nature the restoration presented here is not certain, but it appears that the three bones of the right sclerotic ring are represented, and the extra bone is the second sclerotic plate of the left eye. This is based on Stensiö's interpretation of *B. canadensis* (1948, figs 21, 30), which has been confirmed in the specimen of *Bothriolepis* from Gogo, Western Australia described by Young (1984b), in which the larger of the two posterior sclerotics is on the mesial side. Thus interpreted, both the sensory groove (soc) and the nasal notch (nn) have a mesial position in the restored sclerotic ring of *Nawagiaspis* (Fig. 5A). In this respect it resembles *Bothriolepis* in having the nasal openings notching the sclerotic ring of each side, the other side of the nasal opening presumably notching the lateral margin of the rostral plate (not known). This is in contrast to the condition in *Asterolepis* (e.g. Lyarskaya, 1981, fig. 24), or *Remigolepis* (e.g. Stensiö, 1948, fig. 16), where the nasal openings notch the anterior margin of the rostral plate, and have no connection with the sclerotic ring. However, as argued by Young (1984b), the condition in *Bothriolepis* is likely to be primitive for antiarchs generally.

Paired prelateral and submarginal plates of the cheek, and upper and lower jaw elements from the right side, are also preserved. The prelateral plate (Fig. 7) is of unusual shape, with a much longer anterior process than known in *Bothriolepis*. However, the sensory groove (psoc, Fig. 5C) crosses the plate in much the same position, and the prelateral abutts against the anterior edge of the submarginal in the same manner, as described for *Bothriolepis* by Young (1984b). The submarginal (Fig. 6) is again generally similar to that of *Bothriolepis* (Young, 1984b, pl. 57B, C), with a strong anterodorsal articular process (ad1, Fig.

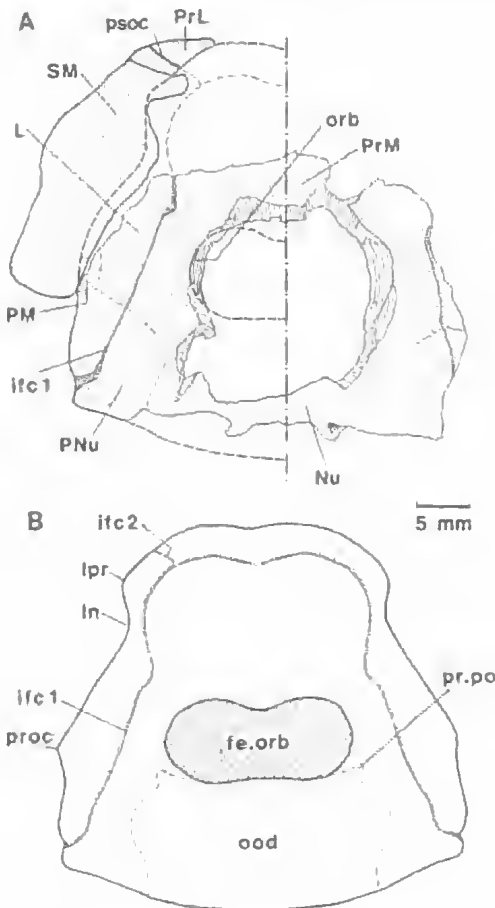


FIG. 4. *Nawagiaspis wadeae* gen. et sp. nov. A, incomplete skull, with left SM and PrL plates in position. B, skull roof restoration, based on A (after the holotype).

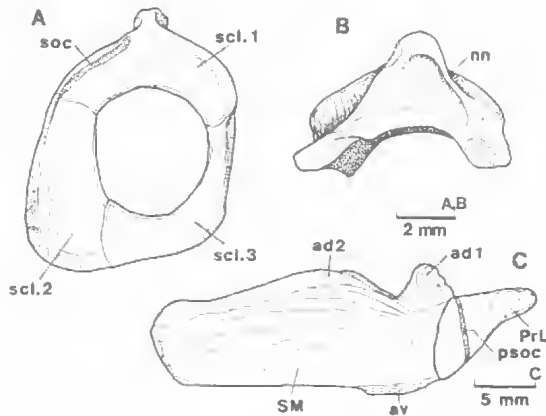


FIG. 5. *Nawagiaspis wadeae* gen. et sp. nov. A, restoration of right sclerotic ring in dorsal view. B, first sclerotic plate from the right side in ventral view. C, restoration of cheek plates from the right side, lateral view (after the holotype).

5C). It differs in being somewhat more elongate, with a straight ventral and convex dorsal margin. The dorsal margin carries a smooth bevelled area where the bone fitted against the lateral skull margin. The ventral margin is thickened at its anterior end to form a ventral articular surface (av), which is shown in the Gogo specimen of *Bothriolepis* to have been in contact with the lateral margin of the subcephalic division of the AVL plate of the trunk, to effect a seal to the branchial chamber when the operculum was closed (Young, 1984b, p. 640). In view of the close similarity in the arrangement of these bones in *Nawagiaspis* to those described by Young (1984b) it is highly probable that *Nawagiaspis* also had an infraprelateral plate, although it is missing from this specimen.

The SO plate differs from that of *Bothriolepis* in being relatively short, with an irregularly notched, near vertical posterior margin (Fig. 9A, B). The excellent preservation clearly shows that this irregular posterior margin is natural, lacking only

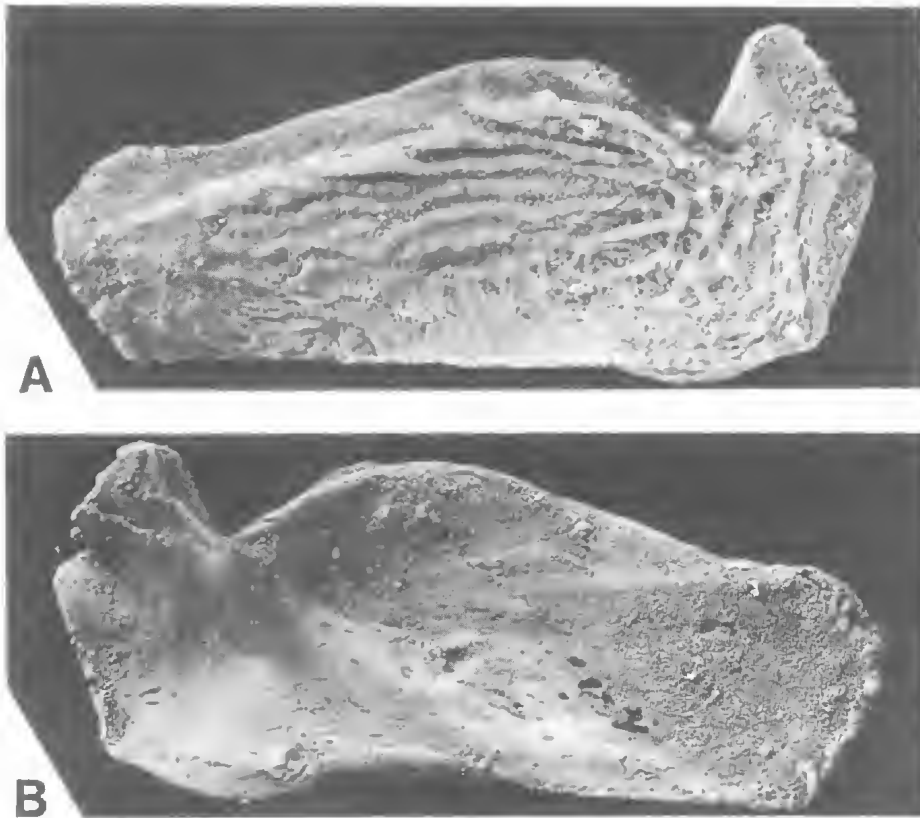


FIG. 6. *Nawagiaspis wadeae* gen. et sp. nov. Right submarginal plate from holotype in lateral (A) and mesial (B) views (x4).

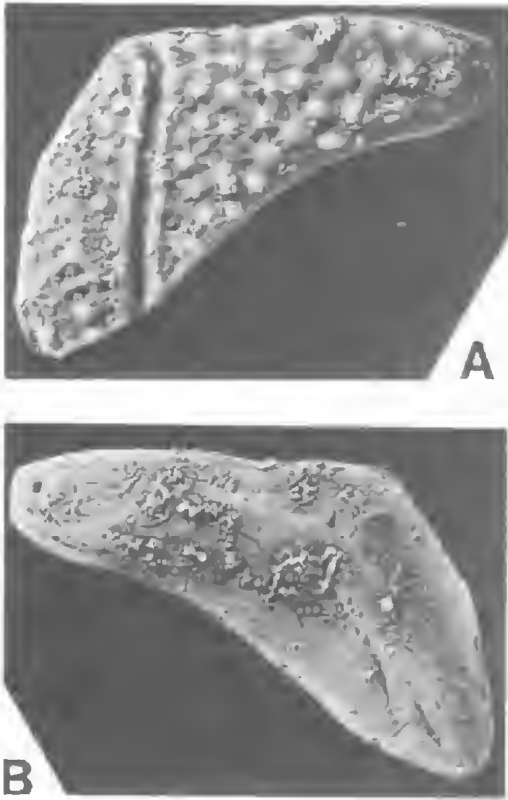


FIG. 7. *Nawagiaspis wadeae* gen. et sp. nov. Right prelateral plate from holotype in lateral (A) and mesial (B) views (x6).

a short posteroventral process (Fig. 8A). There is a smaller dorsal and a larger ventral notch on the lateral margin, a configuration not previously described for antiarchs. However, the bone resembles that of *Bothriolepis* in having a distinct posteroventral process, and a curved biting margin. As such there must have been a deep median notch between the left and right plates as in *Bothriolepis*, and in contrast to other genera where known (Fig. 8). The sensory groove (ifc3) terminates on the plate, in contrast to most other forms where it passes off the lateral margin (Fig. 8D, E). The visceral surface of the bone (Fig. 9B) shows a distinct ridge for supporting the palatoquadrate, as in *Bothriolepis* (Young, 1984b, fig. 3). Also as in that form there is a dorsomesial process forming a flattened area facing the symphyseal plane, which may either have abutted against the SO of the opposite side, or else formed the attachment site for ligaments binding the two sides of the upper jaw together, as has been suggested for *Bothriolepis* (Stensiö 1948; Young, 1984b).

The infragnathal (Fig. 9C, D) resembles that of *Bothriolepis* in all its essential features, although the posterior non-biting portion is proportionately smaller (cf. Young 1984b, pl. 58). A final point is that the biting margins of both the upper and lower jaw elements of *Nawagiaspis* are smooth, in contrast to the serrations seen in *Bothriolepis*.

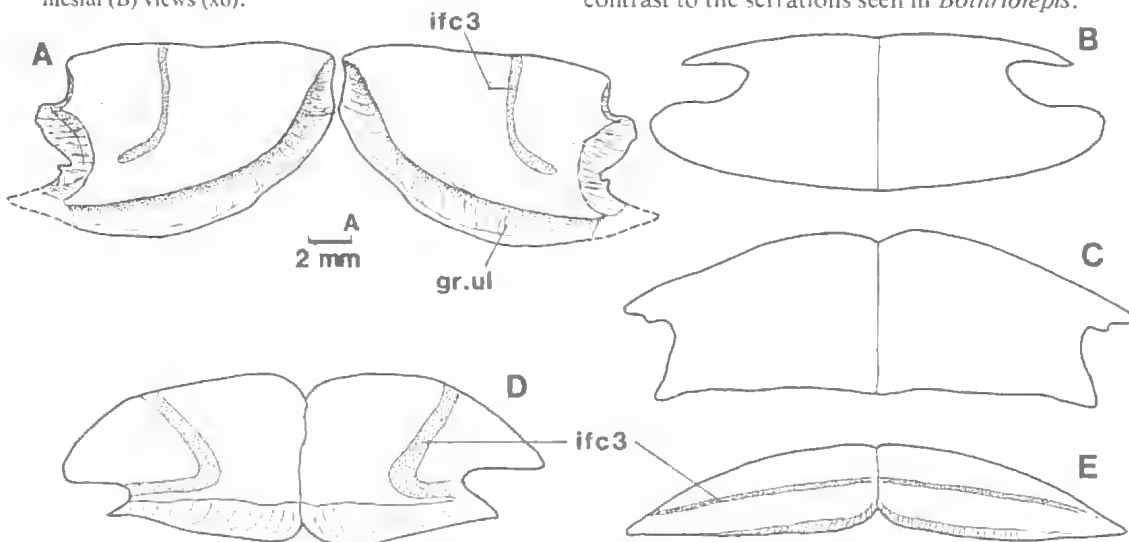


FIG. 8. Paired suborbital ('mental') plates forming the upper biting margin of the jaws in various antiarchs, external view (not to scale). A, *Nawagiaspis wadeae* gen. et sp. nov. (restored after the holotype); B, *Asterolepis scabra* (Woodward), after Nilsson (1941, fig. 5B); C, *Remigolepis* sp., after Nilsson (1941, fig. 6); D, *Pterichthyodes milleri* (Miller), after Hemmings (1978, fig. 6); E, *Asterolepis ornata* Eichwald, based on Lyarskaya (1981, figs 26, 73).

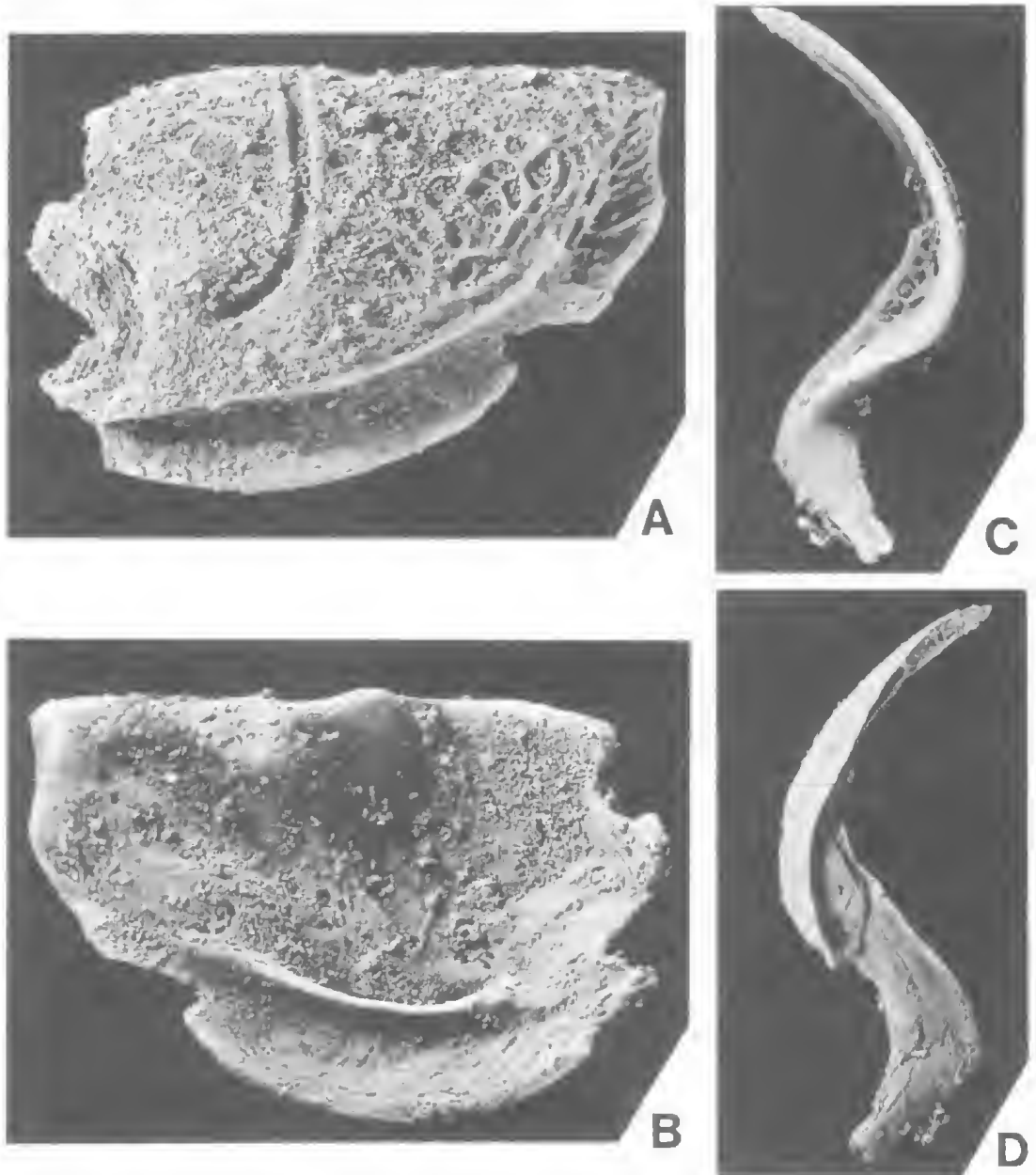


FIG. 9. *Nawagiaspis wadeae* gen. et sp. nov. Dermal bones of the upper and lower jaw as preserved in holotype. A, B, right suborbital ('mental') plate in external and internal views respectively; C, D, right infragnathal bone in dorsal and ventral views respectively (all  $\times 6$ ).

The articulated trunk armour is relatively short and high. The distortion evident in anterior view (Fig. 10B) has been corrected graphically by restoring vertical and horizontal axes to rectangularity, to give angles of about  $115^\circ$  and  $90^\circ$  between dorsal and lateral and lateral and ventral walls respectively. The ventral wall is fairly flat,

and the dorsal wall encloses an angle of about  $130^\circ$  at the midline (Fig. 11B). In dorsal view (Fig. 3) the dorsal wall is notable for its short broad proportions, with a restored midline length of about 47 mm, giving a L/B index of about 78. The dorsolateral ridge is distinctly curved, and in lateral view the midline is strongly arched rostrocaudally,



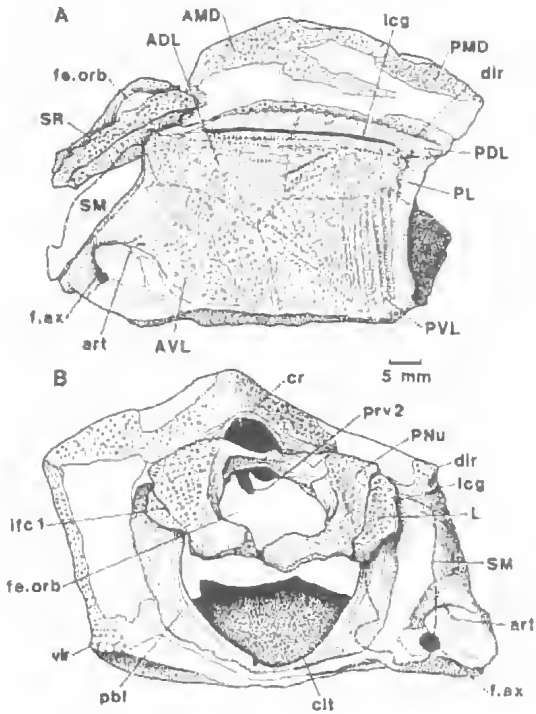


FIG. 10. *Nawagiaspis wadeae* gen. et sp. nov. Holotype in left lateral (A) and anterior (B) views, with position of the left submarginal plate against the trunk-armour indicated by a dashed line.

with the highest point at about the level of the AMD - PMD suture (Fig. 11A), in contrast to many other antiarchs where the highest point is the tergal angle of the AMD plate. The AMD shows only a faint external suture with the right ADL, but internal sutures on both sides are clear, and show that the plate had lateral corners, and was of similar length to, or slightly shorter than, the PMD. The anterior margin is missing but must have been about as wide as the weathered notch in the anterior margin of the trunk armour (Fig. 3), and it is clear that the AMD was not pointed anteriorly as it is in *Asterolepis* and *Remigolepis*. The posterior margin is poorly preserved and its shape is unclear. On its visceral surface the AMD shows a median ventral ridge, which at its anterior end is elevated as a crest (cr, Fig. 11A) behind the small oval pit (pt1) immediately inside the preserved margin. The levator fossa has been lost and is represented by the weathered anterior notch in the specimen.

The PMD shows the median section of the posterior transverse thickening just inside the

preserved posterior margin (cr.tp, Fig. 11A), and it can be assumed that most of the length of the plate is preserved. Externally much of the plate is missing, and plate margins are obscure (Figs 2, 3). In front of the posterior transverse thickening on the visceral surface is a strongly-developed process projecting some 8mm beneath the surrounding bone surface, with the posterior pit facing anteriorly from its anterior surface (pt2, Fig. 11A). In front of this, another equally prominent median ventral ridge is developed (mvr), with a fairly flat ventral surface of cancellous bone which presumably abutted on the vertebral column.

The margins of the ADL are indistinct externally, but the dorsal margin is clear on the visceral surface. The dorsolateral ridge is strongly developed as a row of enlarged tubercles, and part of the obstinate process and main lateral line canal are visible in lateral view (Fig. 10A). Overall, the

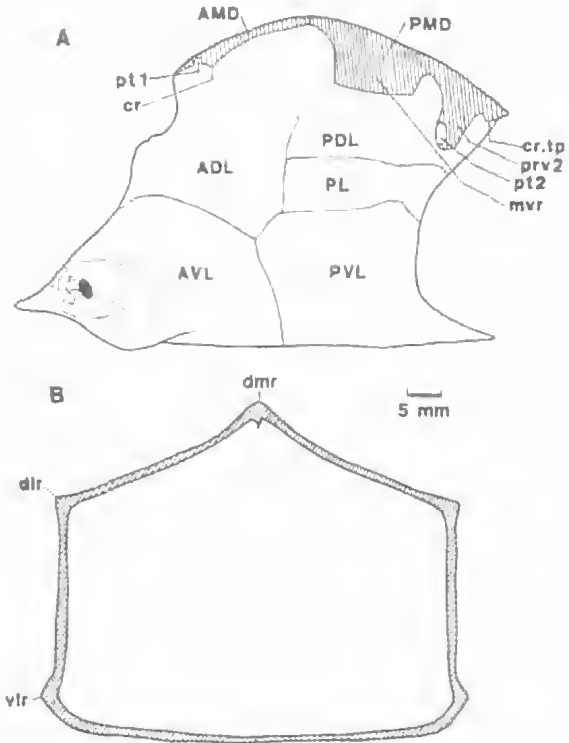


FIG. 11. *Nawagiaspis wadeae* gen. et sp. nov. A, trunk-armour in left lateral view, showing sagittal section through anterior and posterior median dorsal plates of the dorsal wall, and suture pattern for dermal bones of the lateral wall (based on the holotype). B, transverse section through trunk-armour at the level of the anterior dorsolateral plates (restored after the holotype).

lateral wall of the trunk is short and high, with a B/L index of about 66. Its surface is strongly ornamented, and bone sutures are indistinct externally. The tubercles may be aligned in radiating rows, and are fused into vertical ridges inside the posterior margins of the MxL and PVL plates. The suture pattern is clear on the internal surface of the left side, and the four major bones making up the lateral wall are relatively short and high. It is noteworthy that the ADL and PVL are in contact along a short suture, which separates the MxL from the AVL (Fig. 11A). This is the arrangement seen in bothriolepidoid antiarchs, in contrast to the situation in asterolepidoids, where the ADL and PVL are separated by intervening bones. However, the visceral surface also shows what appears to be an incipient suture between the posterior dorsolateral and posterior lateral components of the MxL plate, suggesting that these bones were incompletely fused. A similar situation has been reported in various asterolepidoids, including the Australian species *Sherbonaspis hillsi* as described by Young and Gorter (1981), but in this case the posterior lateral component is extensively overlapped by the AVL. Janvier and Pan (1982, fig. 11) suggested that the 'mixilateral' plate in bothriolepidoids and asterolepidoids was independently derived, in the former by fusion of the PL with the PVL, and in the latter by fusion of the PL with the PDL. As discussed below, the evidence of other characters still indicates independent derivation of the MxL in the two groups, but *Nawagiaspis* shows that in both cases the PL fused with the PDL, and not with the PVL as Janvier and Pan (1982) proposed.

The AVL is incomplete anteriorly, and most of the subcephalic lamina is missing. Noteworthy is the very strong postbranchial lamina (pbl, Figs 3, 10B), which is much better developed than in *Bothriolepis*. The region of the pectoral fin articulation is partly preserved only on the left side. Because of the curvature of the lateral wall this faced anterolaterally rather than laterally. There is a smooth depressed area above an elliptical projection which in lateral view partly obscures the axillary foramen immediately in front. In its position the projection (art, Fig. 10) corresponds to the articular facet posterodorsal to the axillary foramen previously described in an unnamed asterolepidoid from central Australia (Young, 1984b). The margins of the axillary foramen are poorly preserved, but it was evidently smaller than in *Asterolepis* or *Bothriolepis* (e.g. Stensiö, 1931, figs 40-42). The processus brachialis is completely missing from both sides of *Nawagiaspis*. The

lateral lamina of the PVL is preserved on both sides, but the ventral wall of the trunk is badly fractured, and the shape of the MV plate and extent of the subanal lamina of the PVL are unknown. Anteriorly the margins are broken a short distance in front of the postbranchial laminae, so there is no information on whether the semilunar plate was a paired bone, the primitive condition, or a single plate as in *Bothriolepis*.

Suborder ASTEROLEPIDOIDEI Milles (1968)  
Family PTERICHTHYODIDAE Stensio (1948)  
*Wurungulepis* gen. nov.

#### ETYMOLOGY

After the Wurungu aboriginal tribe, another of the original tribes of the Broken River area.

#### DIAGNOSIS

A pterichthyodid with a mid-dorsal length of the trunk-armour attaining at least 100 mm. Trunk-armour triangular in cross-section, with acute angles between lateral and ventral walls at the ventrolateral ridge. Maximum breadth at the level of the ventrolateral ridge, which slightly exceeds height of the trunk-armour.

#### REMARKS

Although poorly known, *Wurungulepis* may be distinguished from other pterichthyodid genera on the basis of trunk-armour shape and proportions as restored below. From *Sherbonaspis* it differs in the apparently higher and deeper AMD, which is probably of similar length to the PMD, the proportionately shorter and deeper ADL, MxL, AVL, and PVL plates, and the more tuberculate ornament. *Pterichthyodes* differs in having a proportionately longer AMD, and a lower and longer trunk-armour which is less triangular in cross-section, with a more narrow ventral surface. *Stegolepis*, *Byssacanthus*, and *Lepidolepis* have an obtuse rather than acute angle at the ventrolateral ridge, with the trunk-armour broader at the level of the dorsolateral ridge than the breadth of the ventral surface. *Byssacanthus* also differs in the proportionately longer AMD, and probably the median dorsal spine, and *Grossaspis* also has a high dorsal spine.

In the development of the trunk-armour *Wurungulepis* most closely resembles the genus *Gerdalepis* Gross. In both there is an acute angle between the lateral and ventral walls of the trunk-armour at the ventrolateral ridge, and the AMD is only slightly longer than the PMD. However, in cross-section the trunk-armour of *Gerdalepis* is higher and narrower, and in lateral

view the PVL is noticeably lower and longer (Gross, 1941, fig. 2), whilst the ornament is of more densely packed tubercles. Whether the peculiar apical chamber of *Gerdalepis* is present in *Wurungulepis* is unknown.

***Wurungulepis denisoni* sp. nov.**  
(Figs 12, 13)

1981 'pterichthyoid-like form', Young & Gorter, p. 90.

**ETYMOLOGY**

After the late Dr R.H. Denison (1911-1985), who made a major contribution to the study of placoderm fishes (e.g. Denison, 1978).

**HOLOTYPE**

QMF16593, an articulated trunk-armour with associated pectoral fin bones and scales.

**LOCALITY**

L4339, north bank of Broken River, GR 640460, Burges 1:100000 sheet (locality 2, Fig. 1).

**HORIZON**

Broken River Formation, Middle Devonian, probably Eifelian (J.S. Jell, pers. comm.).

**DIAGNOSIS**

As for genus (only species).

**DESCRIPTION**

The holotype was collected as a single articulated trunk-armour from which most of the exposed bone was weathered off, although the ventral surface and part of the left lateral side are largely intact. The matrix has been partly dissolved in acetic acid but preparation was discontinued because the bone is badly fractured. Nevertheless a reasonable indication of overall trunk-armour shape can be obtained. The associated bones of the right pectoral fin are indeterminate. During preparation many scales and small bony fragments were released from the matrix.

The trunk-armour is short and broad, and triangular in cross-section (Fig. 12B). Estimated dimensions are: median height, 56 mm; breadth across the ventrolateral ridges, 62 mm; total length 108 mm. The AMD is preserved as a portion of tuberculated bone on the left side, and an impression of the visceral surface on the right. The dorsal-most preserved parts of left and right laminae of the AMD are about 5 mm apart, which suggests that this is close to the median dorsal ridge of the trunk-armour. It is assumed therefore that

there was no median dorsal spine, although this is not certain.

The left lamina of the AMD is important in showing overlap areas for the ADL and MxL plates (oa.ADL, oa.MxL, Fig. 12A). The PMD and MxL plates are missing, but the overlap on the AMD and the level of the posterior margin (as indicated by the PVL plate) place some constraints on the restoration. The PMD must have been short and high, yet probably almost as long as the AMD (Fig. 12A), in contrast to the relative length of these bones in several other pterichthyoid genera (see above). The MxL (or PDL plus PL) must also have

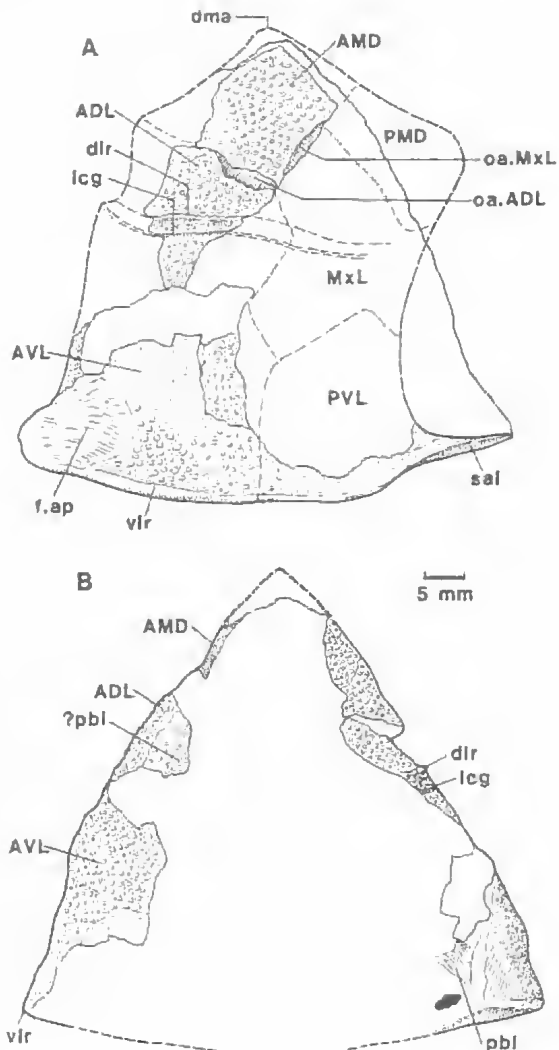


FIG. 12. *Wurungulepis denisoni* gen. et sp. nov. Holotype, QMF16593, an incomplete trunk-armour in left lateral (A) and anterior (B) views.

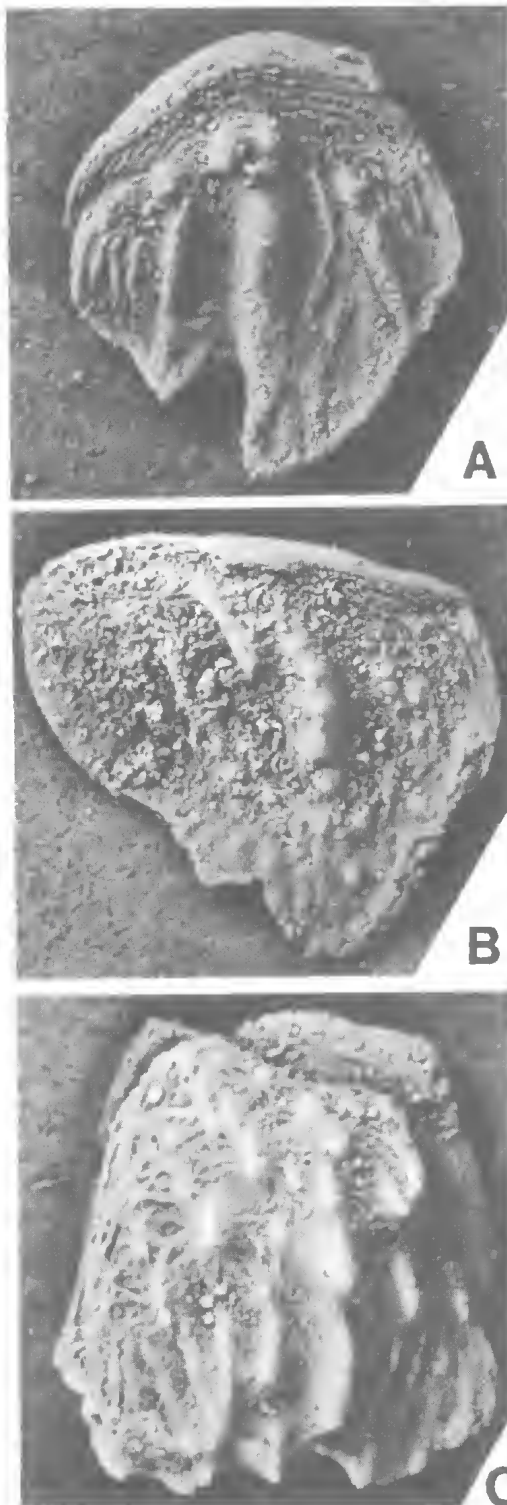


FIG. 13. *Wurungulepis denisoni* gen. et sp. nov. Examples of body scales from the holotype. (A, x18; B, C, x15)

been of short and deep proportions, judging by the shape of surrounding bones.

The ADL is partly preserved on both left and right sides, but only the left gives significant information, with short sections of the dorsolateral ridge and lateral line groove preserved (dlr, lcg). In anterior view the dorsal lamina of the plate is concave, and placed at a very obtuse angle to the lateral lamina. A small unornamented portion of the postbranchial lamina may be preserved on the right side (?pbl). The AVL has a large unornamented area on its lateral lamina (f.ap), which probably represents part of the articular fossa for the pectoral fin. However, the brachial process is missing, and there is no indication of the axillary fossa, which was presumably small as in other pterichthyodids. It is also possible that these structures were placed higher on the lateral wall, above the preserved part, as in *Lepadolepis* (Gross, 1933, pl. 3). The right AVL shows an area of tuberculate ornament, but no other features. Anteroventrally a poorly preserved portion of the postbranchial lamina is shown on the left side (pbl), but the anteroventral margin of the AVL is missing, so the form of the semilunar plate is unknown. Otherwise the ventral surface of the trunk-armour appears to be intact, but is mostly covered by matrix which cannot be readily removed without damage to the specimen. Part of the ventral lamina of the left AVL and PVL are visible in lateral view, the latter showing the full extent of the subanal lamina (sal). Most of the lateral lamina of the left PVL is missing above the ventrolateral ridge (vlr), but its length is indicated by the curvature of the free lateral margin of the subanal lamina. This in turn gives some idea of the length of the MxL and PMD plates, as noted above.

Although much of the bone has been lost from the holotype, it is evident that the component bones of the trunk-armour were short and high, and that the AMD and PMD plates were not greatly different in length. As noted above the triangular cross-section of the trunk-armour is otherwise seen only in *Gerdalepis*, whilst the great breadth of the ventral wall relative to median height is not encountered in any other described pterichthyodid. These features justify the erection of a new genus and species.

The preserved scales in the holotype show that *Wurungulepis* resembled *Pterichthyodes* in its heavy squamation. About a dozen relatively complete scales are available for study, showing a range of variation exemplified by the three illustrated scales (Fig. 13). Most scales have a rounded anterior margin and a pointed posterior

margin. The latter may be irregular, or developed into several posterior processes. On the external surface of the scale is an unornamented anterior rim behind which is a shallow sulcus, corresponding to the overlap area for the preceding scale described by Young (1984a, fig. 8). The ornamented part is covered with irregular tubercles or posteriorly directed ridges. The scale of Fig. 13A is a typical ridged scale, and that of Fig. 13B is an example where tubercles predominate. In both types there is generally an enlarged central ridge, tubercle, or tubercle row just behind the anterior sulcus. This is also a feature of the flank scales of *Pterichthyodes* (Hemmings, 1978, fig. 22C), and of the scales described by Young (1984a). Ventrally these flank scales have an ovate, shallowly-concave base which is generally between a half and two-thirds the length of the scale. In overall proportions these scales vary between slightly longer than broad (Fig. 13A) to up to one third broader than long. In the available sample there are no elongate scales like the ridge scales of *Pterichthyodes* described by Hemmings (1978).

The scale of Fig. 13C differs in its more quadrilateral shape. It has a distinctly depressed overlap area along the anterior and right lateral margin, and a contact face of similar width on the ventral surface inside the posterior margin. This scale presumably came from some restricted region of the body; a few other fragments in the acid residues may belong to similar scales but these may also be broken pieces of dermal bone from the fin exoskeleton.

## DISCUSSION

### RELATIONSHIPS OF THE NEW TAXA

The salient features of *Nawagiaspis* may be summarised in relation to the synapomorphies listed for the major groups of antiarchs by Young (1984c). The following features suggest asterolepid rather than bothriolepid affinity:

1. the tubercular ornament;
2. the general anteromesial direction of the infraorbital sensory canal groove across the paranuchal and lateral plates of the skull;
3. the absence of an extensive preorbital recess;
4. the short anterior postorbital process;
5. the absence of a central sensory canal;
6. (possibly) the short obstantic margin;
7. separate PL and L plates.

On the other hand the following suggest bothriolepid affinity:

8. the lateral position of the nasal openings;
9. the articular process on the SM plate;
10. the lack of a symphysis between the SO plates;
11. the broad anterior margin on the AMD;
12. the common suture between the ADL and PVL.

A decision regarding placement of *Nawagiaspis* depends on which of these similarities are symplesiomorphies, and which are valid synapomorphies. For features of the cheek and jaws this distinction is difficult to make because these aspects of morphology are poorly known in yunnanolepids, the obvious outgroup. In *Microbrachius* the cheek plates are poorly known and the prelateral plate was assumed to be absent by Hemmings (1978) because the concave skull margin resembled that of *Asterolepis*. This argument no longer applies since Lyarskaya (1981) has reported a prelateral in *Asterolepis*, although details of its structure are not available. The most interesting specimen of *Microbrachius* showing the cheek plates is DMSW P513, which as figured by Hemmings (1978, pl. 9, fig. 1) appears to show a space for the prelateral. Watson's earlier interpretation of this specimen (Watson, 1935, fig. 8), clearly shows this notch, and a mesial articular process on the SM plate. I therefore accept this as evidence that the articular process was present in this form, and with reference to the antiarch cladogram of Young (1988) this implies its presence also in *Dianolepis* and *Monarolepis*. The important character for placement of *Nawagiaspis* then becomes the shape of the nuchal plate, and whether it was excluded from the orbital fenestra by the postpineal plate as in *Dianolepis* (and the genus *Tenizolepis* Malinovskaya, 1977, if correctly referred to the bothriolepidoids), or whether it reached the orbital fenestra as in *Monarolepis*, *Grossilepis*, and *Bothriolepis*. Additional material is required to resolve this question.

Denison (1978) did not recognise a pterichthyodid grouping within his 'family Asterolepididae', and Janvier and Pan (1982) regarded *Stegolepis*, *Byssacanthus*, and *Pterichthyodes* as a paraphyletic group because of differences in the breadth of the lateral plate of the skull. Nevertheless, these and the other genera grouped by Young and Gorter (1981) and by Young (1984c, character 33, fig. 2) all conform in having a high short trunk-armour as described above for the new genus *Wurungulepis*. The short and high trunk-armour distinguishes the genera

*Pterichthyodes*, *Gerdalepis*, *Stegolepis*, *Byssacanthus*, *Grossaspis*, *Lepadolepis*, *Sherbonaspis*, and *Wurungulepis* from the low broad trunk-armour of other asterolepids. Outgroup comparison suggests that the short high trunk is the specialised condition, and for this reason a family Pterichthyodidae has been retained here, although clearly additional characters are needed to confirm the monophyly of the group (Janvier & Par, 1982). The resemblance between *Wurungulepis* and *Pterichthyodes* in the ridged ornament on the scales could be a familial character, and, if so, the unnamed form from western Queensland (Young, 1984a) would also belong here. However, this character must remain provisional until the squamation in the other pterichthyodid genera listed above is better known. It should be noted, however, that in *Asterolepis* the scales have a predominantly tuberculate ornament (Lyarskaya, 1977, fig. 6), presumably the primitive condition.

#### BIOSTRATIGRAPHY

Middle Devonian antiarchs from Australia are still very poorly known, but the new forms described here are potentially important because they occur in marine limestones which may be subjected to conodont analysis. Assuming a close phyletic relationship to freshwater forms of similar age, they may provide another tool in correlating marine with non-marine Devonian strata. The new forms described here have little direct contribution to current understanding of Devonian vertebrate biostratigraphy in Australia, but they add to the taxonomic documentation of the faunas, which must proceed if the reliability of correlations and zonation using vertebrates is to be refined.

The Broken River Formation containing these new antiarchs has an age range of Lochkovian (*pesovis* conodont zone) to Givetian (Wyatt & Jell, 1980; Mawson *et al.*, 1985; Mawson, 1987). A detailed analysis of conodont faunas in the Middle Devonian part of the formation is not yet available, and in the Broken River area in the vicinity of the vertebrate localities (Fig. 1) the sequence is complicated by faulting and anticlinal folding, so that no reliable thickness can be ascertained (Wyatt & Jell, 1980). The lowermost Eifelian *partitus* conodont zone has been identified not far from the type locality of *Wurungulepis*, but conodont analysis of this section is again hampered by structural complication and possible debris-flow (allochthonous) contamination (Mawson *et al.*, 1985). It is to be hoped that new

macro- or microvertebrate remains referable to *Nawagiaspis* or *Wurungulepis* will be found in other areas of the Broken River Formation more amenable to detailed conodont analysis (see Mawson *et al.*, 1985).

Young and Gorter (1981) perceived four distinct vertebrate faunas in the Australian Middle Devonian, of which the Broken River occurrences were included as the second youngest. The oldest was considered to be the *Wuttagoonaspis* fauna known from the lower part of the Mulga Downs Group in western NSW, and the Cravens Peak Beds and Lower Dulcie Sandstone in the Georgina Basin in central Australia. Young (1984a) described a small asterolepid antiarch from the Cravens Peak Beds, and suggested that it was the oldest representative of the group in Australia, based on an Emsian age for the *Wuttagoonaspis* fauna. Previously, the oldest asterolepid antiarch was reported to be *Gerdalepis* in the Eifelian Mühlenberg Formation of Germany (e.g. Andrews *et al.*, 1967), which belongs to the *Acinosporites macrospinosis* interval zone of the Eifel sequence, corresponding approximately to the upper *costatus* and *australis* conodont zones of the middle Eifelian (e.g. Streeck *et al.*, 1987).

The possibility that asterolepid antiarchs occur earlier in Australia than elsewhere is of considerable interest, but this depends on the precise age of the *Wuttagoonaspis* fish fauna, which remains problematic. A maximum age for this fauna in western NSW is provided by the underlying marine Cobar Supergroup, which on the evidence of conodonts is largely or entirely of Lochkovian and Pragian age (Pickett, 1980, and pers. comm.). The existence or duration of a time break between the Cobar Supergroup and the overlying Mulga Downs Group containing the *Wuttagoonaspis* fish fauna is controversial, and some elements in the Cravens Peak Beds fish fauna might suggest a younger age within the Middle Devonian (Turner & Young, 1987). This would bring the asterolepid occurrence reported by Young (1984a) and that recorded here from probable Eifelian strata in the Broken River Formation into line with pterichthyodid occurrences elsewhere, which are Eifelian at the earliest (e.g. Denison, 1978). Determining a younger age limit for the *Wuttagoonaspis* fish fauna thus remains an important problem for resolution before the Middle Devonian vertebrate succession of Australia can be clarified.

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